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Forum

Communal life: honest signaling and the recruitment center hypothesis

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The information center hypothesis in animal behavior is lacking both a sound theoretical basis (Richner and Heeb, 1995) and empirical support (Mock et al., 1988; Richner and Heeb, 1995). We suggest that the idea should be abandoned and further research into the evolution of communal roosting or breeding should concentrate on hypotheses that are explicitly based on individual selection. Large benefits at the food patch can arise from group foraging, and we propose here that roosts and breeding colonies may serve as a center where potential foragers can be recruited, and further suggest that display flights and calls at a roost or breeding colony can serve as honest signals used to recruit foragers to a newly discovered food patch. Under the conditions of high patchiness and ephemerality of food sources (i.e., the typical condition for which group foraging may be beneficial), food searching individuals will be widely dispersed and recruitment at a roost or colony may then be more efficient than local enhancement or recruitment at the patch.

The information center hypothesis

Two decades ago, Ward and Zahavi (1973) reached, in a stimulating paper, the conclusion that "communal roosts, breeding colonies and certain other bird assemblages have been evolved primarily for the efficient exploitation of unevenly-distributed food sources by serving as information centres." The general view at the time was that the function of communal roosting or breeding is its efficient protection from predators (e.g., Lack, 1968). Zahavi (1971) proposed that the predator avoidance function of bird roosts and breeding colonies is of minor importance compared to the foraging advantage through the information center mechanism first described by Ward (1965). A main problem of the information center hypothesis has been Ward and Zahavi's (1973) claim that the information center function of roosts has been the driving force for the evolution of roosting behavior. The difficulty was to explain, without being a group selection argument, why a successful forager should return to the roost and thereby pay the time and energy cost of the trip from the food patch to the roost and back, and furthermore suffer from the cost of being followed by parasitic, unsuccessful foragers.

The information center hypothesis holds that information is exchanged at the roost or colony concerning the location of ephemeral and patchy food sources. A forager that is unsuccessful on one occasion can follow a successful forager when leaving the roost, and will in turn be followed on the occasions when it foraged successfully. It therefore assumes that the altruistic act of informing unsuccessful foragers will be reciprocated in the future. However, reciprocal altruism requires that the costs of giving information are small compared to the benefits of receiving information, that individuals that give information on one occasion are likely to receive information on the following occasion, and that nonreciprocators can be identified and excluded (Trivers, 1971, 1985). These stringent conditions make reciprocal altruism in large assemblages unlikely. Additionally, it has been shown recently that high mobility of individuals (as is typical for roosts) limits the potential for cooperation (Enquist and Leimar, 1993; Houston, 1993), and this further reduces the probability that a roost can function as an information center.

Ward and Zahavi (1973) further suggested that the aerial display and formation flights serve to advertise the location of the information center to conspecifics (Ward, 1978; Ward and Zahavi, 1973). They argued that the spectacular aerial displays at the roost or at preroost gatherings, as is typical for many species (Zahavi, 1971) [e.g., swallows (*Hirundo rustica*), bee-eaters (*Merops superciliosus*), starlings (*Sturnus vulgaris*), and pink-footed geese (*Anser brachyrhynchus*)], may not only advertise the roost to conspecifics but also to predators, and communal roosting could therefore not have evolved for its predator avoidance function. However, given the fact that roost location is often stable over weeks or months [e.g., 3 to 20 weeks per season in starlings (*S. vulgaris*) and common grackles (*Quiscalus quiscula*), and the same sites are used in successive years (Caccamise et al., 1983); roost location of carrion crows (*Corvus corone*) and jackdaws (*C. monedula*) is stable over years (Richner and Heeb, personal observations)] it is equally hard to see why birds should continue to advertise its location. Also it is not clear which direct benefit an individual could obtain that would compensate for the cost of advertising, and how nonadvertising cheaters could be excluded. A new explanation for the displays (Zahavi, 1983) holds that "a bird which displays with others is able to assess its potential to compete with its flock members when they would eventually reach the feeding site." Displaying would allow a bird to find feeding mates that match its competitive potential or, preferably, are weaker competitors at the food patch. This function of the displays, however, cannot explain how cheaters could be excluded, and displaying would therefore not be stable.

The "two-strategies hypothesis"

The two-strategies hypothesis (Weatherhead, 1983, 1987) suggests that information transfer is the main advantage of communal roosting for inferior foragers (e.g., subordinates), whereas successful foragers benefit by reducing their predation risk by obtaining central roosting positions where they are buffered from predators by the surrounding subordinate birds. The hypothesis suggests that communal roosting evolved through the benefits at the roost to the superior foragers and it is therefore based on individual selection. The information parasitism by the subordinate birds is merely the price that dominants are willing to pay for having access to safe roosting positions. This hypothesis requires the assumptions that the superior foragers can assure better roosting positions, and that successful foraging depends on an intrinsic quality of an individual (i.e., dominance) rather than on the chance discovery of a good food patch on a given day. Since only dominant individuals are efficient in finding the ephemeral and patchily distributed food sources, the two-strategies hypothesis greatly limits the efficiency of a roost or colony-based exploitation strategy. The hypothesis explains the aerial displays observed at roosts as the advertisement of social status in order to get access to the safe roosting sites. The display

remains an honest signal since "a successful individual cannot deceive other roost members of its success without behaving as a subordinate bird and thereby losing its advantage in roosting communally" (Weatherhead 1983).

The recruitment center hypothesis

Evans (1982) first pointed out that the benefits derived from group foraging are more likely to favor a colony-based foraging system than the mechanism proposed by the information center hypothesis. The benefits derived from group foraging may outweigh the costs of giving away information on food location, and could therefore explain why successful foragers return to a communal place. Evans (1982) also observed that, when leaving the communal place, some flock leaders called to attract other colony members and others did not, but he could not provide an explanation for these differences in vocal behavior.

In order to substantiate our claim that roosts and colonies can serve as recruitment centers, we will emphasize three points: (1) that the recruitment center hypothesis can explain why successful foragers should return to a roost or breeding colony and give away information; (2) that the recruitment center hypothesis can account for the aerial displays by the "honesty-by-cost" principle of Zahavi (1975, 1977); and (3) that the recruitment center hypothesis can explain why some flock leaders call and others don't.

Why and when should successful foragers return to the communal place once a food patch has been discovered? First, the net benefit of group foraging (B_G) plus the time and energy cost of the return trip (C_R) must be higher than the benefit of staying at the patch and foraging singly (B_S)

$$B_G + C_R > B_S$$

and second, recruiting other foragers at a roost or colony ($R_{R/C}$) has to be more efficient than passive accumulation of birds at the patch [i.e., local enhancement (L_E)] or active recruitment at the patch [i.e., local recruitment (L_R)]

$$R_{R/C} > L_E + L_R$$

Numerous benefits can arise to an individual foraging in a group, as opposed to a single forager. Group foraging may reduce the risk of predation by the simple dilution effect or by earlier detection of a predator (e.g., Charnov and Krebs, 1975; Kenward, 1978; Powell, 1974; Seyfarth et al., 1980), reduce the risk of starvation (Ekman and Hake, 1988), reduce the time spent in predator vigilance (Barnard, 1980; Caraco, 1979; Caraco et al., 1980; Elgar and Catterall, 1981; but see Elgar, 1989; Pulliam, 1973), and increase feeding time and feeding rate (e.g., Lendrem, 1984) by various mechanisms such as prey confusion, social learning (Avery, 1994; Krebs et al., 1972; Pitcher et al., 1982), use of public information (Valone, 1989, 1993), and others [for a general review see Pulliam and Caraco (1984)]. A cost of foraging in a group is that the potential benefits (A) at the food source have to be shared among the n individuals of the group. Without further benefits from group foraging, the net benefit to the individual is therefore A/n^1. Many of the effects mentioned above will reduce food competition, individual need for vigilance, predation risk, etc., and the net benefit to the individual feeding in a group will therefore be higher than A/n^1 (i.e., $A/n^{<1}$). The benefits of group foraging also increase with increasing scarcity (e.g., Clark and Mangel, 1984) and ephemerality of food patches. High ephemerality of relatively rich food sources will reduce the effects of food competition since the duration of a food source is not strongly correlated with its rate of exploitation. Under such conditions of low food competition it may not be highly relevant to an individual to feed in a group of optimal size, but it may still be relevant to forage in a group for the reasons given above. However, an ideal free distribution of birds among patches is also not expected, and therefore the net benefits to the individual are likely to vary among foraging groups.

When should foragers be recruited at the roost or at a colony? A successful forager wishing to benefit from feeding in a larger group may stay at the food patch and wait for other birds to join (i.e., local enhancement), or it may actively attract other birds to the patch (i.e., local recruitment) by calls or other displays, or it may return to the roost or breeding colony to recruit other foragers (i.e., colony-based recruitment). The decision between these options will be influenced by the respective recruitment efficiencies and the costs of the three mechanisms. Under conditions of high patchiness and ephemerality of food, searching individuals may be widely dispersed, and it is then likely that recruitment at the roost or colony is more efficient than waiting at the food patch for other birds to join or recruiting them locally.

In summary, the successful foragers could benefit by using a communal site for recruiting conspecifics to their newly discovered food patch, and the less successful foragers could benefit by gaining information concerning food discoveries and then follow the most promising individual. The recruitment center hypothesis could therefore, through the various benefits at the food patch, explain why successful foragers return to a roost or colony and provide information on food location.

How should a successful forager recruit other birds at the roost or colony? As shown above, the information center hypothesis does not offer a convincing argument of why birds should perform aerial displays at the communal site. In contrast, the hypothesis that communal roosting or breeding evolved through the recruitment center function of roosts and colonies can explain this behavior, and in fact these displays strongly support the recruitment center hypothesis. Imagine some successful foragers returning to a roost or colony to recruit other individuals to their food source. Given that the net benefit to an individual is likely to vary among foraging groups, it will pay to compare the returning birds on the basis of the given recruitment signals. The problem of an individual that seeks information is then to find out which bird is the best one to follow. Since aerial display in general can be costly (e.g., Hails, 1979; Mather and Robertson, 1992; Møller, 1991) it has the potential to be used as an honest signaling system. The birds that, having discovered a patch, can derive the highest net benefit by an increase in feeding group size, are the ones most willing to engage in escalated displays. The follower will, among equal competitors at the food patch, achieve the same benefit as the advertising individual, and therefore the advertising signal can be an indication of the benefit that a follower may obtain. With unequal competitors a follower may further take into account the competitive qualities of an advertiser in relation to its own competitive qualities when deciding who to follow.

Can the recruitment center hypothesis explain why some successful foragers advertise and others don't? A successful forager that seeks recruits should advertise it strongly, but a forager that is already feeding in a group of a size where a further increase in group size does not change the net benefit should be silent. Since a bird that has no knowledge of a food patch when leaving the roost or colony will also be silent, it poses the problem to potential followers to know which one of the silent birds is the one that knows a patch. If birds cannot discriminate between the two types, then the only option is to follow the advertisers. The existence of two types of silent birds (i.e., birds that do not advertise because they do not know a food patch, or because they know a patch but are not looking for more recruits) does not affect the honesty of ad-

vertising. Elgar (1986), in the context of recruitment at a food patch, has convincingly shown that singly feeding sparrows are able to use fine-graded calling depending on their interest and benefit of group feeding, and calls at colonies that led to mass recruitment to the food patch have also been observed in other species (Stoddard, 1988). Successful but silent foragers may appear at roosts because of antipredator benefits (e.g., Lack, 1968) or other advantages that arise from communal roosting. In breeding colonies they are obliged to return for feeding their chicks. Without such benefits or obligations they may stay away from the communal site as long as they are not looking for recruits or are being recruited. Investigating recruitment displays and calls at roosts and colonies in the context of the recruitment center hypothesis will certainly be rewarding in future studies.

The recruitment center hypothesis requires only a few general assumptions and leads to testable predictions. The assumptions are that food sources are patchily distributed in space, show ephemeral appearance in time, and that food within the patch is relatively abundant. These three conditions will reduce the effect of increasing food competition as group size increases. In contrast, with homogeneous and predictable food distribution the task of food finding is comparatively easy and a recruitment center-based foraging strategy is not superior to foraging singly. The main predictions are (1) that the net benefit of a forager at the food patch is higher after returning and feeding with the recruits than when previously feeding without the recruits, and (2) that birds will stop recruiting other birds at the communal site when no additional benefit can be achieved by a further increase of feeding group size. An experimental test would consist of creating ephemeral food patches and measuring the benefits of a marked bird at the patch at the initial discovery and after returning from the roost or breeding colony with the recruits. The recruiting signals at the colony are expected to be initially strong and then cease at subsequent returns. The benefits may be experimentally influenced, for example, by changing predation pressure that makes group feeding beneficial through a reduction in the individual need for being vigilant. An increasing predation pressure predicts further recruitment of foragers.

The main difference between a communal roost and a breeding colony consists of the fact that a breeder is obliged to return to the breeding colony to feed its chicks even if there is no interest for further recruits, whereas in communal roosts a bird is free to go back or roost elsewhere. A bird that has no interest to recruit more coforagers will go back to the roost only if additional benefits arise from communal roosting (e.g., Lack, 1968; Weatherhead, 1983). For roosts the return schedules are dictated by external factors such as nightfall or high tide, whereas in breeding colonies the return schedules are more or less given by the state of hunger of the offspring.

In summary, the recruitment center hypothesis proposes that the recruitment center function of roosts or breeding colonies for the successful foragers may be an overlooked selective force for the evolution of a colonial lifestyle. Further, the aerial displays during the arrival or departure of birds at the roost or colony have the potential to be honest signals indicating to unsuccessful foragers that a food patch has been located, and these displays may also indicate the net benefit that a recruit may obtain at a food patch. Interestingly the recruitment center hypothesis hinges on another important concept of Zahavi (1975, 1977, 1987), the "honesty-by-cost principle" of signaling (see also Grafen, 1990), which is amenable to experimental testing in the context of forager recruitment. We do not claim that the mechanism proposed here is the only or most important selective agent leading to the evolution of communal roosting or breeding, but suggest that further studies investigating the evolution of this behavior should concentrate on the two hypotheses that are explicitly based on individual selection: the two-strategies hypothesis, which is based on the benefits to a successful forager at the roost, and the recruitment center hypothesis, which is based on the benefits that accrue to successful foragers from recruiting other individuals at a roost or colony to their food patch.

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